

Variation and Incipient Speciation in the African Buffalo

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Receipt of Ms. 5. 11. 1971

I. Introduction

Although interest in the history of Africa's biota continues to develop, knowledge of speciation in African mammals has hardly advanced beyond a stage reached nearly 40 years ago, and we still have little information concerning the evolution of even the largest and most conspicuous animals.

Among these, the African buffalo (*Syncerus caffer*) presents one of the more striking examples of incipient speciation, in view of its well differentiated forest and savanna populations. In this preliminary survey it is intended to reconcile some divergent views on the nature of geographic variation in the buffalo and then to suggest how this might be interpreted in terms of the species' history.

Forest and savanna buffaloes are so different in size and appearance that for some time they were considered to belong to separate species. LYDEKKER (e. g. in 1913) was among the first to recognise the existence of intergradation between the morphological extremes. No less than 43 specific and subspecific names associated with known type localities had been given to buffaloes (ALLEN 1939) and LYDEKKER assigned these to two groups of subspecies, a *nanus* group (predominantly forest animals) and a *caffer* group (savanna only). The names *brachyceros* and *aequinoctialis*, the status of which was to become controversial, were both assigned to the *nanus* group.

SCHWARZ's (1920) arrangement also involved a single species, but subspecies were arranged in three groups (Table 1), with *brachyceros* and *aequinoctialis* together in a separate category from *caffer* or *nanus*.

DOLLMAN (in LYDEKKER 1926), following some observations of CHRISTY, retained LYDEKKER's groups as species, but transferred *aequinoctialis* to the *caffer* group. He gave a useful summary of the subspecies that were considered valid at that date.

CHRISTY (1929) reduced the number of subspecies to three (plus one which he did not formally name, although it was distinguished on his map, p. 451) but continued to assert that there were two separate, allopatric species, *nanus* and *caffer*. His was one of the few pioneer attempts to explain geographic variation in an African mammal in historical and ecological terms, though now his work requires some re-assessment. CHRISTY's (1929) treatment of his subspecies *Bubalus nanus nanus* (Table 1) calls for comment. Extreme specimens were referred by him to "*reclinis*" and "*planiceros*" classes, regardless of their relative size or provenance. In specimens placed in the first of these informal categories, the horns converge and may even cross at the tips, while the distal half of the shaft is much narrower than the proximal. In "*planiceros*" the horns are broader and much more divergent. *Reclinis* is a strict synonym of *nanus*, as it is based on the same type; some buffaloes that are here referred to *brachyceros* (i. e. *aequinoctialis* of CHRISTY) were assigned to *reclinis*. The type of *planiceros* is from an unknown locality but appears to represent the very worn horns of a *brachyceros*-like buffalo and should not have been placed by

Table 1
Comparisons between various classifications of African buffaloes

present arrangement	SCHWARZ 1920	CHRISTY 1929	MALBRANT 1936	BLANGOU 1954	SCHOUTEDEN 1945
<i>Syncerus caffer nanus</i> , sensu lato, in part.		<i>S. (= Bubalus) nanus nanus</i> - forest subgroup in part.		<i>nanus</i> group - <i>S. c. bylaeus</i> in part.	<i>S. n. adolfifriederici</i> .
ditto.	<i>nanus</i> group - <i>S. caffer bylaeus</i> .	<i>S. n. nanus</i> - forest subgroup in part.	<i>nanus</i> group - <i>S. c. nanus</i> .	<i>nanus</i> group - <i>S. c. bylaeus</i> in part.	<i>S. n. nanus</i> in part.
ditto.	<i>nanus</i> group - <i>S. c. nanus</i> ; <i>S. c. diehli</i> ; etc.?	<i>S. n. nanus</i> - forest subgroup in part - forest margin forms?	<i>nanus</i> group - <i>S. c. nanus</i> .	<i>nanus</i> group - <i>S. c. nanus</i> .	<i>S. n. nanus</i> in part.
ditto.		<i>S. n. nanus</i> - forest outskirts subgroup in part.		<i>sylvestris</i> group - <i>S. c. cottoni</i> (i. e. <i>simpsoni</i>)	<i>S. n. simpsoni</i> .
ditto.		<i>S. n. nanus</i> - forest outskirts subgroup in part.	<i>nanus</i> group - <i>S. c. sylvestris</i> .	<i>sylvestris</i> group - <i>S. c. planiceros</i> .	
<i>S. c. brachyceros</i>	<i>nanus</i> group - <i>S. c. adamauae</i> ; <i>S. c. thierryi</i> ; <i>S. c. beddingtoni</i> ; <i>S. c. planiceros</i> ; <i>brachyceros</i> group - <i>S. c. brachyceros</i> in part; <i>S. c. bouyi</i> ; etc.?	<i>S. n. aequinoctialis</i> in part.	<i>nanus</i> group - <i>S. c. savanensis</i> .	<i>savanensis</i> group - <i>S. c. brachyceros</i> .	<i>S. caffer brachyceros</i> .
<i>S. c. brachyceros/aequinoctialis</i> intergrades.	<i>brachyceros</i> group - <i>S. c. brachyceros</i> in part.	<i>S. n. aequinoctialis</i> in part.			

present arrangement	SCHWARZ 1920	CHRISTY 1929	MALBRANT 1936	BLANCOU 1954	SCHOUTEDEN 1945
<i>S. c. nanus/caffer</i> intergrades		<i>S. n. nanus</i> - forest outskirts group in part.		<i>aequinocialis</i> group - <i>S. c. mathewsi</i> .	<i>S. c. mathewsi</i> .
<i>S. c. nanus/caffer</i> intergrades.				<i>savannensis</i> group - <i>S. c. christyi</i> (nomen nudum).	
<i>S. c. aequinoctialis</i>	<i>brachyceros</i> group - <i>S. c. aequinoctialis</i>	<i>S. n. aequinoctialis</i> in part.	<i>caffer</i> group - <i>S. c. aequinoctialis</i> .	<i>aequinocialis</i> group - <i>S. c. aequinoctialis</i> .	<i>S. c. aequinoctialis</i> .
<i>S. c. caffer</i>	<i>caffer</i> group - <i>S. c. caffer</i> .	<i>S. caffer</i> .		<i>caffer</i> group - <i>S. c. radcliffei</i> .	<i>S. c. radcliffei</i> .
<i>S. c. caffer</i>	<i>caffer</i> group - <i>S. c. caffer</i> .	<i>S. caffer</i> .		<i>caffer</i> group - <i>S. c. caffer</i> .	<i>S. c. caffer</i> .

CHRISTY in his "Bubalus nanus nanus". Diebli SCHWARZ, 1913 was also assigned to *planiceros* by CHRISTY but the type skull appears to be of an aged forest buffalo, perhaps representing a forest/savanna intermediate.

CHRISTY's view that his species *nanus* and *caffer* only converged in form and appearance in the White Nile region was not acceptable to MALBRANT (1935) who believed that intermediate types occurred over a wider area. MALBRANT (1936) and BLANCOU (1935) showed that two distinguishable savanna populations, a western and an eastern, met in the area of the Chari basin, Tchad. These animals had all been included under the name "*Bubalus nanus aequinoctialis*" by CHRISTY, who had however relegated the names applicable to the western form to "*Bubalus nanus nanus*" (*S. c. nanus*) though one of these names, *brachyceros* of GRAY, 1837, has priority over *aequinocialis*, of BLYTH, 1866.

BLANCOU's 1954 classification, developed from an earlier one (BLANCOU 1935), was complex and involved four hierarchial levels. Like MALBRANT (1936) he made a point that will be supported here, namely that *aequinocialis* is closer to *caffer* than to *brachyceros* or *nanus*. His scheme attempted to deal with the morphological and geographical intergradation between forest and savanna buffaloes, but no account was taken of secondary intergradation, and some of the measurements he presented were misleading.

SCHOUTEDEN (1946) distinguished two separate species of buffalo, though these were not coextensive with those of CHRISTY (Table 1). SCHOU-

TEDEN's well illustrated account suggests that some at least of the subspecies that continue to be recognised by BLANCOU (1954) might well be valid, and eight were recognised by SCHOUTEDEN within the Congo (Kinshasa).

Table 1 summarises these different approaches. Other commentaries on buffalo taxonomy have been superseded by the ones listed there, or have applied to limited areas of Africa and will be referred to in the ensuing discussion where an attempt will be made to sort out conflicts between these taxonomic arrangements.

II. Material

Over 280 skulls or frontlets with horns have been examined (IFAN Museum, Dakar; British Museum [Natural History], London - BM; Powell Cotton Museum, Birchington, Kent - PCM; Game and Wildlife Department, Ghana).

Illustrations of additional specimens are available especially in CHRISTY (1929), BLANCOU (1935 and 1954), SCHOUTEDEN (1946), MALBRANT and MACLATCHY (1949) and DEKEYSER and DERIVOT (1957). Data on a further 1200 skulls or pairs of horns are provided mainly by HOLLISTER (1924), BLANCOU (1935), DALIMIER (1947), MALBRANT and MACLATCHY (1949) and BEST and EDMOND-BLANC (1969). Different measurements are employed by different authors so it has not been possible to make as much use of these data as might be desirable.

Most of the specimens and data available are from males, as females have been collected less frequently. In the discussion below, the comments on geographical variation apply to males unless otherwise stated.

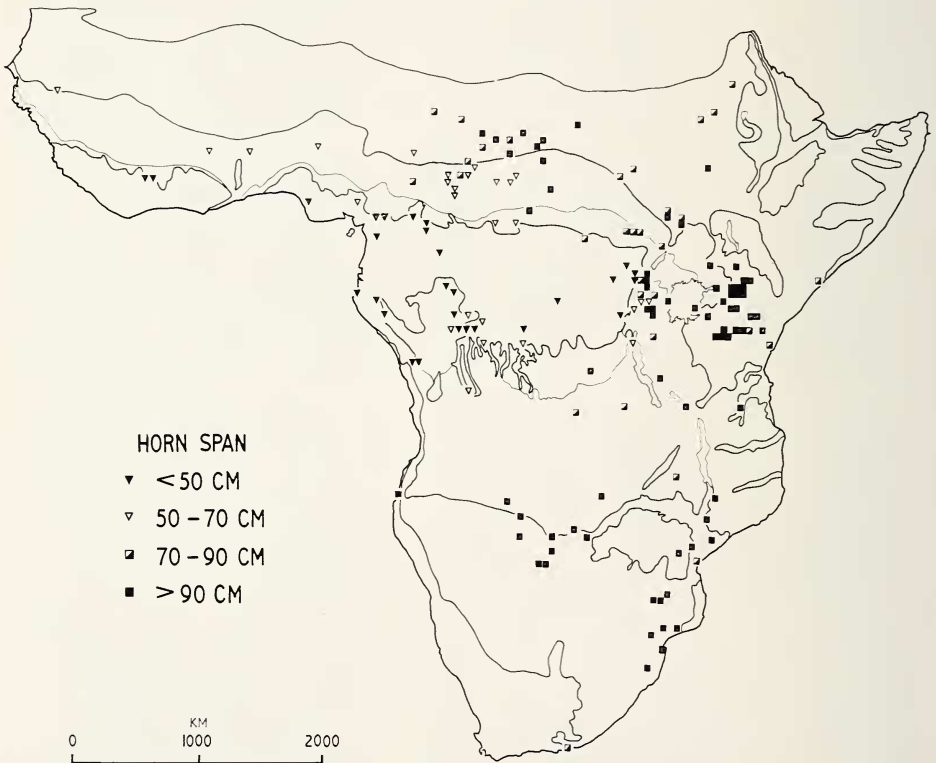


Fig. 1. Map of Africa with boundaries of vegetation zones (after MOREAU, 1966, from KEAY) showing distribution of horn-span classes in male buffaloes, derived from means of available records from half degree \times half degree squares

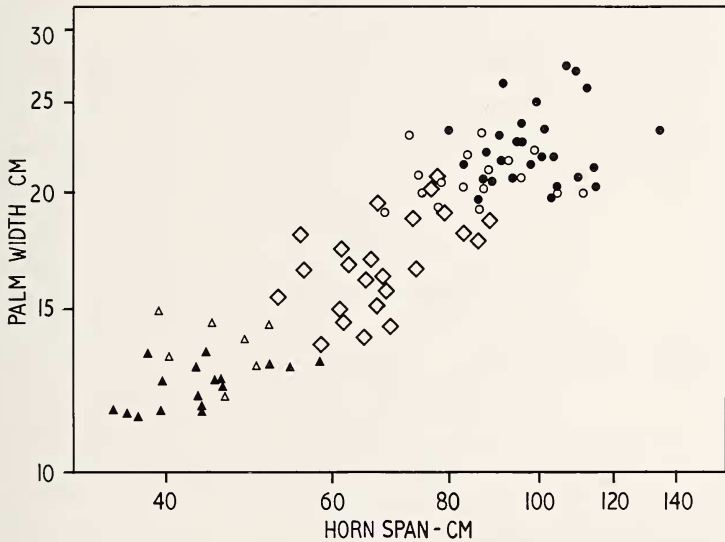
III. Geographic variation

Buffaloes show a greater range of morphological variation than do any other vertebrate species in Africa. Geographic trends contributing to this variation can be assessed by plotting the means of variates from local populations on a distribution map. The most widely available datum is the span of the horns in the adult male, and the distribution in Africa of four arbitrarily chosen horn-span classes is shown in figure 1.

Buffaloes of the largest size class occur in the savanna of Tchad and Sudan south to Natal and west to Angola. The smallest animals, forming a second group, come from the Congo and Guinea forest blocs and from the forest and savanna mosaic of the lower Congo. Suitable data from the southern Congo and northern Angola are sparse. Similarly there are few records from the West African savanna, but here it is apparent that the animals are much smaller than the East African savanna buffaloes and form a third and intermediate category. It thus appears that we can recognise three chief size groups each with a wide distribution corresponding to a distinct ecogeographic region of Africa. The groups are each designated by the oldest available name:

1. *Nanus* group — small forest forms;
2. *Brachyceros* group — intermediate, West African savanna forms;
3. *Caffer* group — large, Eastern and Southern African savanna forms;

These categories should be regarded as "subspecies groups" and their informal



- △ forest buffaloes from edge of forest in Cote d' Ivoire;
- ▲ forest buffaloes from edge of forest in Camerun and Congo Brazzaville;
- ◇ savanna buffaloes from localities in West Africa, Senegal to River Chari;
- savanna buffaloes from River Chari to Sudan and Ethiopia;
- savanna buffaloes from East Africa south to Mozambique.

Fig. 2. Scatter diagram of horn span plotted against width of horn at base ('palm width') on log scale for male buffaloes

recognition should not prejudice the formal recognition of subspecies within each category.

In the *nanus* group, the general colour of animals of both sexes is light reddish brown, with darker markings (see illustration in ROSEVEAR 1938) though some individuals are blackish. For instance less than 10 per cent of a sample of 140 forest buffaloes from N'Dende, Gabon, were of this latter morph (MALBRANT and MACLYATCHY 1949). The horns are relatively short and lie in the facial plane or rise above it, and their length is greater than their maximum span. Weights of three adult males from N'Dende were 270, 280 and 290 kg and an adult female scaled 265 kg (MALBRANT and MACLYATCHY 1949). Several subspecies may belong in this group, but their delineation cannot be established here.

Buffaloes of the *brachyceros* group are larger in all respects. The horns, which are also relatively larger than in the *nanus* group, are more divergent, so that horn span is somewhat greater than horn length, and they dip slightly below the facial plane. Most adults are of the dark morph. For example, I observed only 4 or 5 red animals in a herd of over 60 at the Mole Reserve, Northern Region, Ghana. There does not appear to be more than one subspecies in this group.

Caffer group animals are larger again and the horns diverge from the sagittal plane at an angle of about 150° so that horn span is still greater than horn length. The orbital rims are more tubular and the skull is relatively shorter, wider and more massive than in other "groups". The frontal region is swollen into a convex boss to accommodate the basal expansions of the horns which in the largest males form a cowl over the top of the skull (Figure 10). The horns curve down and away from the skull well below the facial plane (a tendency to be seen in females as well). These skull and horn features, most clearly expressed in males, are partly developed in the *brachyceros* group of buffaloes as well, which in all respects are intermediate

between the *nanus* and *caffer* groups. For the latter animals, body mass is very much greater than in forest buffaloes. SACHS (1967) gives ranges of 661 to 849 kg (mean of 751 kg; for eight males from the Serengeti); 701 to 835 kg (six males from Kenya; data from MEINERTZHAGEN); and 426 to 468 kg (two adult Serengeti females). Two subspecies (*caffer* and *aequinoctialis*) are recognisable but are probably no more distinct from each other than are some of the regional populations in the *nanus* group. The light or red morph appears to be absent from adults except where there is intergradation with other populations.

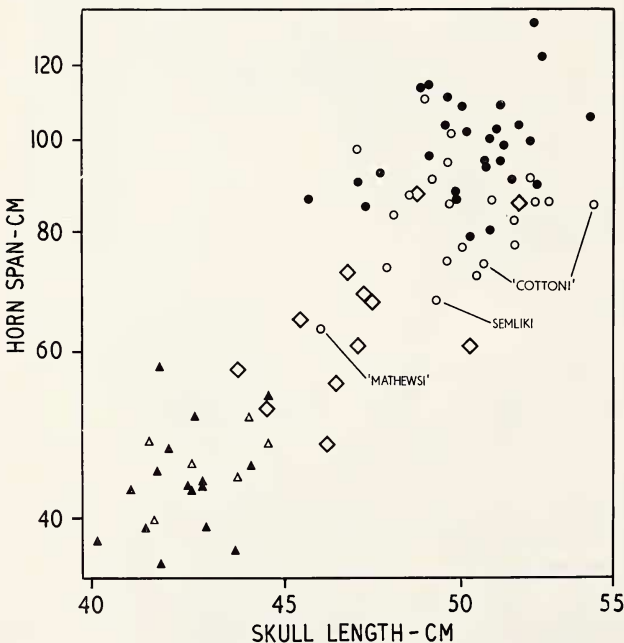


Fig. 3. Scatter diagram of horn span plotted against skull length on log scale. Symbols as in figure 2, but intergrades between forest and savanna buffaloes also shown

Table 2
Means and standard deviations of horn and skull measurements (in mm) of male buffaloes
Numbers in samples bracketed

Subspecies	Greatest span of horns	Length of (longest) horn along curve	Width of horn at base	Greatest length of skull	Width of skull across mastoid processes
<i>Syncerus caffer nanus</i>	455 ± 58.4 (35)	474 ± 67.3 (21)	128 ± 9.75 (21)	426 ± 10.7 (22)	215 ± 11.7 (21)
<i>S. c. nanus</i> , Ituri forest (= <i>adolphiriedericti</i>)	388 ± 35.7 (4)	380 ± 11.7 (4)	134 ± 7.12 (4)	415 ± 13.6 (4)	225 ± 6.83 (4)
<i>S. c. brachyceros</i>	675 ± 72.6 (23)	601 ± 61.1 (23)	166 ± 18.3 (25)	455 ± 22.9 (15)	240 ± 7.34 (11)
<i>S. c. aequinoctialis</i>	843 ± 79.9 (16)	739 ± 102 (15)	212 ± 17.2 (16)	500 ± 18.2 (17)	270 ± 20.9 (15)
<i>S. c. caffer</i>	973 ± 119 (49)	898 ± 103 (31)	224 ± 21.5 (29)	503 ± 17.9 (31)	282 ± 18.0 (28)
<i>nanus/brachyceros</i> intermediates (?): type of <i>beddingtoni</i> (BM 99.10.23.4) topotype of <i>bunti</i> (from LYDEKKER 1913) BM 35.6.7.1	580	565	175	—	—
aff. <i>bunti</i> , Lokoja (from LYDEKKER 1913) BM 16.7.6.1	—	521	184	—	—
	—	510	168	447	240
	—	495	191	—	—
	482	520	128	462	229
<i>nanus/caffer</i> intergrades: type of <i>cottoni</i> (PCM Cong. 316) PCM Cong. 326	860	—	255	—	—
PCM Cong. 412	745	720	221	508	302
BM 25.5.24.1	865	780	228	543	280
type of <i>matbewesi</i> (BM 4.5.19.1)	683	530	191	493	272
	643	705	167	461	259

Bivariate plots of measurements indicate the segregation of the three groups, but reveal extensive overlap between samples from a single group (Figures 2, 3). Tables of measurements also indicate the limited overlap between the groups (Table 2). The biological relations between the subspecies groups can be examined by surveying geographic variation across Africa, region by region.

In attempting to describe and assess variation with the small samples available it is not always easy to decide whether a morphological series truly indicates a geographical trend or whether it merely reflects individual variation within a single population. A particular morph, on which perhaps a scientific name has been based, may represent the mode in one population but be an extreme in another and thus it may be very difficult to decide where on a (geographic) clinal scale the population represented by one specimen should lie.

IV. Regional variation

a. West Africa

LYDEKKER (1913) recognised the races *planiceros* (= *centralis*), *beddingtoni*, *thierryi*, *hunti* and *brachyceros* in West Africa (listed from west to east), though KOLLER (1935) appears to have accepted *planiceros* and *thierryi* only. LYDEKKER's names are less soundly based than those of SCHWARZ (1920) for they are partly established on effectively individual differences in colour, also used as key features (p. 291). LYDEKKER thought that the type of *centralis* GRAY, 1872 (probably from Gambia) resembled the type of *planiceros* BLYTH, 1863 (locality unknown), and that the former was therefore a synonym. The horns of the frontlet which is the *planiceros* type are very worn and show no closer resemblance to the *centralis* type than do other savanna buffaloes from West Africa. Indeed skulls, with horns, from Senegal (BM), Northern Region of Ghana, "Nigeria" (BM 61.1060; 51.709) and Republic Centrafricain (PCM) as well as some of those without locality, possibly from Cote d'Ivoire or Guinée, illustrated by DEKEYSER and DERIVOT (1957), are all similar and should be assigned to *brachyceros*, the earliest available name, of which *planiceros* and *centralis* are to be regarded as synonyms. Senegalese buffaloes should not be assigned to *aequinotialis* (DEKEYSER 1956; DUPUY 1969). *Thierryi* is based on a female from Pama, Upper Volta, (11° 15' N 0° 45' E) with a horn span of 610 mm which is therefore larger than the female type of *brachyceros* (horn span 488 mm) but still referable to that form (see Table 2) as a synonym.

In West Africa BLANCOU (1954) recognised, the races "*planiceros* (*sylvestris* group)" and "*brachyceros* (*savannensis* group)" as well as "*nanus*" (*nanus* group — see Table 1). He states that *brachyceros* ranges west to Cote d'Ivoire and *planiceros* reaches as far east as Nigeria, both in the forest margins and savanna. There does not seem to be much support for this arrangement and indeed there is as yet no evidence even for clinal variation of *brachyceros* with longitude.

On the other hand *brachyceros* surely intergrades with smaller forest buffaloes. *Beddingtoni* from Ashanti and *hunti* from Southern Nigeria are on the small side for *brachyceros* (Table 2) and may represent *nanus/brachyceros* intermediates. The same may be said for a specimen from Lokoja referred to *hunti* (LYDEKKER 1913), a male from Wushishi (BM 35.6.7.1.), and the type of *adamauae* (SCHWARZ 1914a). A specimen collected by HUNT from Southern Nigeria (BM 16.7.6.1.) which is perhaps a topotype of *hunti* is even smaller in horn dimensions, which bring it into the range of *nanus*. The type of *diehli* (SCHWARZ 1913) from Mamfe may also be in this category but horns obtained by MONARD (1951) at Ndiki and Dioma, north of the

Sanaga river, are well within the range of *nanus*, though referred by that author to "*sylvestris*". Such forms could conceivably represent a "forest outskirts" category as mapped for West Africa by CHRISTY (1929) or a "*sylvestris* group" (MALBRANT 1935). But although large savanna and small forest buffaloes are very different, there is a degree of overlap between their measurements and single skulls cannot always be referred with certainty to one subspecies rather than the other. It does not seem reasonable therefore to recognise an additional "forest outskirts" subspecies in West Africa, and this view will receive further confirmation below.

DEKEYSER and DERIVOT (1957) illustrate buffalo skulls from the edge of the Guinea forest bloc in Cote d'Ivoire and these specimens, which I have re-examined, conform to the small forest *nanus* type. RAHM (1961) also notes a small forest buffalo from Asagny, near the coast. It is not known whether the population of the Dahomey Gap which links these forest buffaloes with those of Southern Nigeria tends towards a forest or a savanna form. Small forest buffaloes were obtained by Heslop (BM uncatalogued) from Warri province, southern Nigeria (horn span 430 mm, average of three) and presumably these are connected with the *nanus* population of Cameroon to which *nuni* MATSCHIE, 1913 belongs.

b. Cameroon-Tchad region

In the region of the Chari-Ubangi watershed, the distinction between forest and savanna buffaloes has been recognised for some time (MALBRANT 1935, MALBRANT and MACLATCHY 1949, BLANCOU 1935, 1949, 1956) but the apparent cline between these populations has been expressed in a variety of ways.

Thus CHRISTY (1929, plates 1-3), relying on the evidence of specimens from several parts of the Congo basin, distinguished forest, forest outskirts and "bush" (i. e. savanna) forms. His last two categories are heterogenous groups (Table 1). Some of the skulls of "forest" buffaloes are either immature or female, not male as stated, though this does not necessarily prejudice the recognition of a dwarf forest race. CHRISTY nevertheless demonstrated the increase in size between forest and savanna populations, and the wording of his key to plates suggests that a fourth category, a forest margin form, was to be recognised, though he did not map its distribution.

MALBRANT (1935) described the sequence in the chad region in terms of three types — *Syncerus caffer nanus* (dense forest), *S. c. sylvestris* (open forest and forest edge) and *S. c. savannensis* (savanna). He gives little information on the geographic ranges or morphology of these types, and indeed *sylvestris* and *savannensis*, as *nomen nova*, are not identified to type specimens and localities.

BLANCOU's (1954) classification conforms with MALBRANT's terminology, while recognising additional extralimital races within the latter author's three divisions. In 1958, when he simplified his scheme and abandoned the additional races, BLANCOU adopted the name *hylaesus* of SCHWARZ instead of *nanus* and specifically substituted *savannensis* for *brachyceros* on the grounds that *nanus* and *brachyceros* could not be traced to particular localities. "*Nanus*" is without locality but it is unquestionably based on a specimen (BM 606 a — a frontlet with horns), and has therefore a much better claim to acceptance than many other early names for large mammals. "*Brachyceros*" is based on two female skulls from Bornu and the name should certainly not be rejected. A male skull was apparently also brought back by the collectors, DENHAM and CLAPPERTON, but was never available for study (CHRISTY 1929).

A different approach to the classification of chad and Cameroon buffaloes was made by SCHWARZ. In describing several forms from this area he implicitly recognised that they represented a morphological series (SCHWARZ 1913, 1914 a, 1914 b, 1929)

Table 3

Arrangement of nominal subspecies of West African buffaloes as reflected by Schwarz (1913, 1914 a, 1914 b, 1920). Except where stated the specimens are in the Senckenberg Museum, Frankfurt. The sequence begins with the smallest forest specimens and ends with the largest savanna ones.

name	habitat	known localities
<i>hylaesus</i>	forest	Molundu — type locality; Yendi Plateau; Bonda river, Assobam forest.
<i>nanus</i>	?	? (BM 606 a).
<i>diebli</i>	forest (near edge)	Mamfe — type and only locality.
<i>adamauae</i>	Guinea savanna	Garua on Benue river (type locality); east of Kontago, Northern Nigeria (BM 10.24.5.22).
<i>beddingtoni</i>	?	"Ashanti".
<i>planiceros</i>	Sudan savanna?	"Senegambia" (BM 65.3.30.1).
<i>houyi</i>	Sudan savanna	Pelle — type locality; Gore; River Nanya Barya; between Bosum and Bate; Bate.
<i>brachyceros</i>	Sudan savanna	Bornu — type locality (BM 605 a).
" <i>brachyceros</i> "	Sudan and sahel savanna	Fort Lamy (BM 7.7.8.253). Baguirmi, between Mugur and Mahr (Mougour and Mere?); Baguirmi, northeast of an east-west line connecting Adamawa and Wau (BM 10.5.16.1); Badingua.

which has an eco-geographical basis to it as well, following the forest-savanna sequence (Table 3). It seems unlikely that we can describe this cline by using so many named taxa when at the same time individual variation is so great. As will be suggested later, animals referred by SCHWARZ to *brachyceros* may not represent a northward extension of the clinal sequence.

Before attempting an independent evaluation of the cline between forest and savanna buffaloes, which is reconstructed in figure 4, it will be necessary to consider variation within the forest populations. Extremes in size are illustrated in figure 5, representing "*hylaesus*" (smallest) and "*simpsoni*" (largest) morphs, and intermediates. The smallest buffaloes are apparently from the depths of the forest, SCHWARZ (1914 a) having described *hylaesus* (see Table 3) from a male skull with a horn span of only 350 mm. There are so few records from well within the Camerun-Gabon forest that it is impossible to be certain of the status of *hylaesus*. It may well prove to be a valid race.

Small morphs (horn span between 350 and 400 mm) are also known from Cape Lopez (BM uncatalogued) as well as from Fernan Vaz and Divenie (Gabon) and Nagonamanga (Rio Muni), if the photographs of MALBRANT and MACLATCHY (1949) and BASILIO (1962) are correctly interpreted. Small buffaloes are also recorded from places much closer to the forest margin and from the forest-savanna mosaic of the lower Congo (PCM; SCHOUTEDEN 1946, MALBRANT and MACLATCHY 1949) but

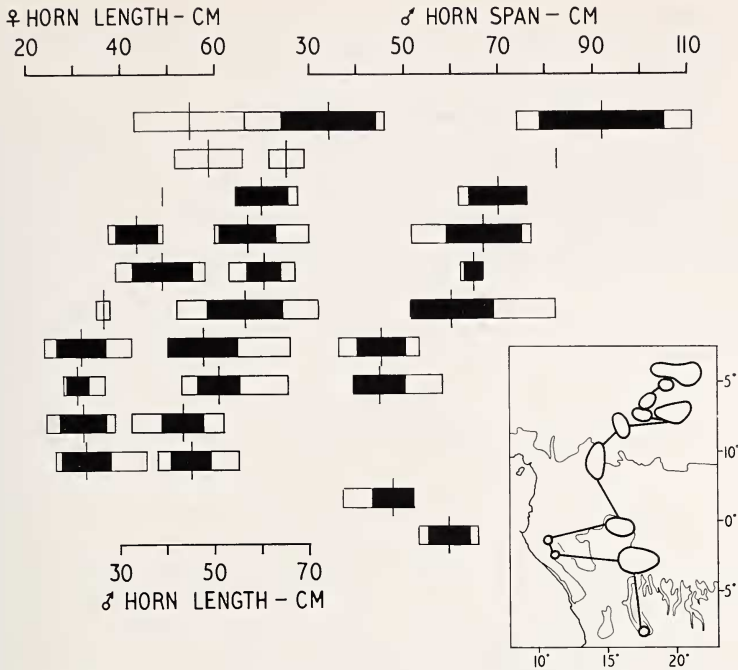


Fig. 4. Measurements of horn length along curve for females and males; and of horn span for males only; of samples of buffaloes from West Central Africa. Each symbol indicates the mean, one standard deviation from the mean and the range of values. The records are presented from north to south (top to bottom) from localities as follows (each circled in the inset map): 1 - North of the River Chari, 2 - 9°30', Tchad, 3 - north of 8° Tchad, 4 - 7°50' to 8° N, Tchad, 5 - 7° N, 19 - 20° E Republic Centrafricain, 6 - 6 - 7°50' N, 15°30' to 17° E, Republic Centrafricain, 7 - 3 - 5° N, Camerun, 8 - 0 - 1° S, Congo Brazzaville, 9 - Sandara, Gabun, 10 - N'Dende, Gabun, 11 - 2 - 3° S, Congo Kinshasa, 12 - Franz Josef waterfall, Congo Kinshasa — Data are taken from Powell Cotton Museum, BLANCOU (1935), MALBRANT and MACLATCHY (1949) and SCHOUTEDEN (1945)

series from Sindara, N'Dende and N'gounie, the Batouri region of Camerun and the Makoua region of Congo (Brazzaville) include many medium sized specimens as well, that is with horns spanning between 400 and 500 mm in the males (see figure 4).

Large morphs (horn span more than 500 mm) represent intermediates between the *nanus* and *brachyceros* types north of the forest and on the south side of the Congo

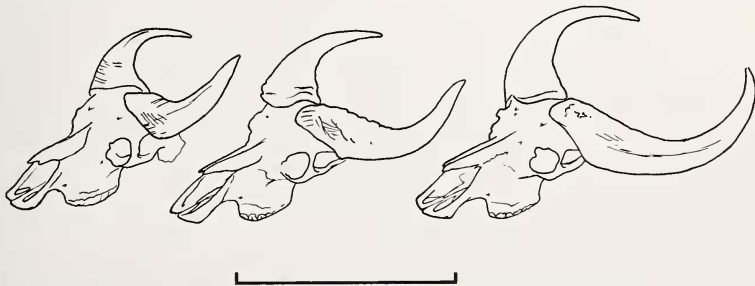


Fig. 5. Skulls of forest buffaloes *Syncerus caffer nanus* sensu lato from (left to right): Cape Lopez, Gabun (BM uncatologued); Libouna, Congo Brazzaville (PCM - FC 56); M'Boko, Congo Brazzaville (PCM - FC 108). The scale indicates 0.5 m

bloc they are known as far into the forest as M'Boko ($0^{\circ} 15' S 15^{\circ} 10' E$ – PCM) as well as from several localities in the Lower Congo valley. Similar large animals occur across the belts of riverrain forest of the southern Congo and will be discussed below.

While there is a broad overlap in the geographical range of the arbitrarily defined largest and smallest size classes of forest buffaloes, it appears that larger individuals are more characteristic of the forest edge or areas beyond the forest proper, and small ones within the forest itself. But when one examines *populations* it becomes apparent that there is also a wide variation within any local sample (figure 4), and it is difficult to relate sample differences to habitat differences. It is thus impossible to analyse clinal trends in detail without many more data. Most of the samples of *nanus* are from the forest edge and these may in reality average larger than the deep-forest types, so the question of the status of *hylaenus* is still in doubt.

In comparing savanna and forest buffaloes, however, a difference is conspicuous; the former are clearly larger than the latter (figure 4) in the Cameroon-Centrafrican region. Once again overlap in measurements between *nanus* and *brachyceros* popu-



Fig. 6. Skulls of male savanna buffaloes from (top left to right): Senegambia (*Syncerus caffer brachyceros* - BM 11.6.10.112); Mole Game Reserve, Ghana (*S. c. brachyceros*); Fort Lamy, Tchad (*brachyceros* / *aequinoctialis* intergrade - BM 7.7.8.253); southeast of Melfi, Tchad (*S. c. aequinoctialis* PCM N Chd 140); Meshra 'er Req, - BM 44.137 (*S. c. aequinoctialis* - BM 44. 137). The scale indicates 0.5 m

lations makes it impossible to identify a regionally distinctive third and intermediate race.

Buffaloes on the southern edge of the forest appear to "repeat" what occurs in the north, as some tend to be as large as *brachyceros*. Few data are available and the status of the animals will be discussed below.

If larger and smaller races are to be differentiated from *nanus* itself, a problem of nomenclature arises. The type of *nanus* is, overall, of "medium" size, though the horns diverge at such a small angle that they only span 380 mm, below average for most of the *nanus* group and bringing it into the *hylaesus* range. It would be most inconvenient, however, if the name should be given priority over *hylaesus* should the latter prove valid. Thus to ensure its continued use for the better-known buffaloes of the forest/savanna mosaic its type locality is here restricted to this habitat in the Congo valley below Kinshasa.

c. Chari valley

Savanna buffaloes from north of the river Chari at first appear to continue the forest-savanna cline (figure 4). Visitors to the Chari basin have however agreed that there are two distinct forms of buffalo in the area, as well as intermediates (BLANCOU 1935, MALBRANT 1936). The two types (*brachyceros* and *aequinoctialis*) are segregated very approximately to the south and north banks of that river respectively. Southwest and west of the Chari, over nearly 35° longitude (3,000 km) savanna buffaloes are also of the *brachyceros* form; similarly across nearly 20° longitude (2,000 km) northeast and east of the Chari, they are unquestionably of *aequinoctialis* type (see figures 6, 7, 8). The races appear to be relatively uniform and except in the Chari-Congo watershed itself show little overlap in measurements (figure 4; table 2). Intermediates occupy a zone running approximately northwest-southeast from Lake Tchad to the Congo forest. Rather than indicating a stage in a cline, this zone

appears to be a region of secondary intergradation. It is often difficult to distinguish intergrades from "typical" *brachyceros* or *aequinoctialis* specimens, especially as populations of intermediates may include animals morphologically typical of either type. An arbitrary distinction has been made on the basis of horn width — those skulls with horns less than 20 cm in maximum transverse breadth are assigned to the western race and others to the eastern one. Using this typological distinction the distribution of races is mapped in figure 8, and it is found that SCHWARZ'S (1920) assignment of large buffa-

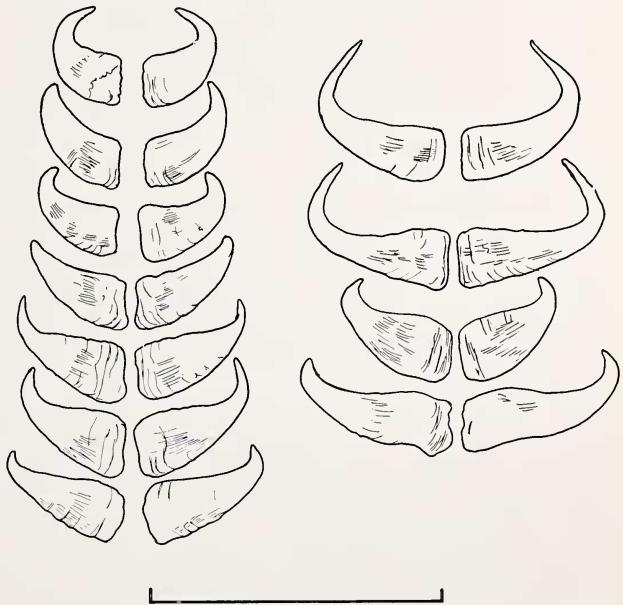


Fig. 7. Horns of male buffaloes from (left) southwest of the Chari river, and (right) north of the Chari river. The scale indicates 1 m

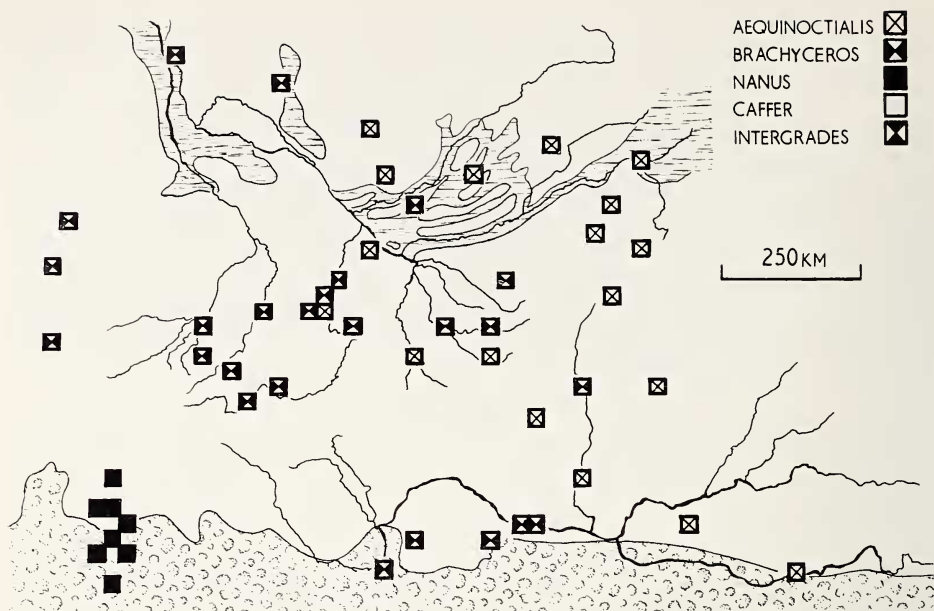


Fig. 8. Map of the Chari-Ubangi watershed and the Chari valley, from 15—27° E, 3—12° N, showing distribution records of buffaloes assigned to various subspecies (see text). Areas subject to seasonal flooding (above), and forest (below) shaded

loes from localities just northeast of the Chari in Tschad (Table 3) to *brachyceros* appears to be confirmed. The female skulls on which the name *brachyceros* is based and male skulls reportedly from the same general locality, Bornu, (KOLLER 1935) are however not as large as the specimens to which SCHWARZ refers and these latter should properly be regarded as intergrades between *brachyceros* and *aequinoctialis*.

South of the Chari, buffaloes of *brachyceros* form are recorded as far east as Bria, 22° E (BLANCOU 1949, figure 7), Ndele, 20° E, the Bamingui basin, about 19° E, and Tongbu (= Tungbo), 20° E on the Ubangi (BM 7.7.8.254 — SCHWARZ was unclear as to the affinities of this specimen because of his concept of *brachyceros*). Buffaloes tending toward *aequinoctialis* in appearance, with wide spreading horns, more than 20 cm in width at the base, are recorded as far west as Fort Crampel, south of the Chari at 19° E (BLANCOU 1935) and Bedadi, 18° E, to the north of that river (PCM). A specimen from the latter locality is indistinguishable from animals from Lado, 1700 km to the southeast. Further southwest across the Chari, buffaloes are mostly of the *brachyceros* type (figure 7) but some with broader horns tend towards *aequinoctialis* and the large form *houyi* from 16° E may also show some affinity with the latter.

d. Southern Congo and Angola

According to HILL and CARTER (1941) buffaloes of the *caffer* group occur in Angola as far north as Chitau (11° 15' S, 17° 01' E) and those of the *nanus* group range south to Bengo, the type locality of *mayi* of MATCHIE, 1906 (8° 50' N, 13° 45' E) which is based on a female with a horn span of 400 mm, relatively large for the *nanus* group (Table 2). *S. c. simpsoni* was named from further east (LYDEKKER 1910), at Pama in the Kwilu valley (4° 14' S, 18° 21' E). The type is a female with a horn span of 330 mm (BM 10.5.27.1) and another topotypical female (BM 38.7.18.2) has a horn span of 270 mm. These animals are not atypical for *nanus*, though a topo-

typical male (BM 38.7.18.3) with a horn span of 540 mm is large for the group. From further south, on the Franz-Josef waterfall (7° 34' S, 17° 14' E), SCHOUTEDEN (1946) illustrates fairly large buffaloes with divergent horns (spanning 590 mm, average of four). CABRAL (1967) believes that the buffaloes in the Luando Reserve (about 11° S, 17° E) are of the *simpsoni* type. JOBAERT (1957) reports a male with a horn span of 540 mm from the Loange valley (about 22° E) but while he records "*simpsoni*" from some localities in Kasai (JOBAERT 1949) he cites records of "*nanus*" from most of this region. CHRISTY (1924, 1929) illustrates a male of the *nanus* group from Bakambuli, the Sankuru river, southern Congo, (4° 59' S, 23° 26' E) also with large horns, and another from the Lomami river, central Congo (c. 25° E). Finally a specimen from Kibanga, Lake Tanganyika (4° 29' S, 29° 09' E), with horns spanning 508 mm (BM 29.4.23.2) also belongs to the *nanus* group, though occurring outside the main forest bloc (figure 9).

BLANCOU (1954) uses the name *cottoni* for these relatively large buffaloes but the name is wrongly applied, both for typological and geographical reasons. Though these animals approach the *brachyceros* group in size, they are below the average and have more slender horns, yet they are in turn large for the *nanus* group. Animals of similar type extend sporadically as far north as M'Boko in Congo (Brazzaville) but probably only as the largest individuals in the locality. It seems impossible at the moment to define the area where *simpsoni* buffaloes become the norm within the population.

SCHOUTEDEN (1945) maps the ranges of his species *caffer* and *nanus* (see table 1), which for the southern Congo correspond to the subspecies groups recognised here. He records confrontation between *caffer* and *nanus* only in Central Kasai, with *caffer* continuing well up into the forest margin in Katanga. Localities listed by JOBAERT (1954) further corroborate SCHOUTEDEN's map. The ranges of the two groups also come close together in Angola but here *nanus* extends rather further into the savanna. The apparent absence of a wide ranging population of intermediate forms perhaps corresponding to *brachyceros* in appearance suggests that we may be dealing with another zone of secondary intergradation. Indeed some "*simpsoni*" buffaloes may represent intergrades. BLANCOU (1949) refers to intergrades between *cottoni* (i. e. *simpsoni*) and *caffer*, calling them "*christyi*" (nomen nudum), but he gives no details of such animals.

e. Sudan

From figures 2, 3 and table 2 it is apparent that *aequinoctialis* is much closer in its dimensions to *caffer* sensu stricto than to *brachyceros* and it is distinguished from the former chiefly by its horn dimensions, which never attain the high values shown by some *caffer* specimens (Table 2). The horns of *aequinoctialis* tend to be shorter, less deflected below the frontal plane and narrower at the base, the horn "palms" being flatter and less inclined to form a massive convex boss. However, there is considerable overlap in measurements and to identify a skull by seeing whether or not the horns reach below the basioccipital plane is not an infallible guide to geographic provenance, contrary to what is stated by BEST and EDMOND-BLANC (1969).

The two forms presumably intergrade over a broad area between L. Albert and L. Rudolf. Large savanna buffaloes from the Albert Park, N. E. Congo, are closer to *aequinoctialis* than *caffer* (DALIMIER 1947; table 2). A BM specimen (uncatalogued) from the Lorian swamp in N. E. Kenya has flat horn bases much like *aequinoctialis*, and the type specimen of *S. c. radcliffei*, now apparently lost, was described as having the horn bases flattened and diverging rather than parallel, suggesting a resemblance to *aequinoctialis*. Again this last criterion does not provide a diagnostic feature, and the type locality, Burumba (1° 00' S, 30° 50' E), is well within typical

"*caffer*" country (MOREAU, HOPKINS and HAYMAN 1946). *Radcliffei* has indeed come to be used as a name for the largest East African buffaloes (SCHOUTEDEN 1945).

Heavy horned buffaloes, nearer *caffer* sensu strictu, are recorded from as far north as the Mongalla region (PCM Sud.-1, 43) and one enormous specimen from the Torit region (BM 44.137) is large even for typical *caffer*, though it may be incorrectly labelled.

Interbreeding between Sudanese savanna buffaloes and the smaller Congo forest animals is not well documented, but the zone of intergradation must be narrow, as *aequinotialis* is recorded from the very edge of the Congo forest bloc (SCHOUTEDEN 1945, figure 9). Female buffaloes shot at the head of the River Nepoko (about 2° 50' N, 27° 15' E) and assigned to the "forest outskirts" group (CHRISTY 1924) may represent intergrades. A little further to the north of the extreme northeast corner of Congo, Kinshasa, in the Faradje-Niangara area, CALONNE-BEAUFAICT (1916) recorded that buffaloes were all of the dark variety, but that still further north between the River Uele and the Sudanese and Centrafricain borders, a proportion of adults were of the red morph. This may reflect intergradation with *brachyceros* buffaloes or with forest buffaloes occurring outside the main Congo forest bloc. Red forest buffaloes, presumably of the *nanus*-group are recorded from the Zandi region of the southern Sudan near the Congo border (DANIELL 1950). Though DANIELL's figures not certainly of adult animals, other authors agree that an enclave of the forest form occurs in this locality (WOODMAN 1952, MACKENZIE 1954). Another forest species, the giant hog *Hylochoerus meinertzhageni*, also has an isolated population in the wooded mountains of the southern Sudan (FORBES 1948, MACKENZIE 1954).

CHRISTY (1929) saw a resemblance between certain Sudan savanna buffaloes and "*nanus*", but the particular example he illustrates (BM 5.9.21.1) is, I find, a subadult *aequinotialis* with horns that have not completed growth.

BLANCOU (1949) has suggested that intergradation between forest and savanna buffaloes may be complex, with demes of one type isolated from the main population and intergrading with other forms, but gives no details.

f. Southern and Eastern Africa

A boundary between nominal races *radcliffei* and *caffer* is drawn about 3° S in East Africa (SCHOUTEDEN 1946) or somewhere between the Limpopo and the Zambezi (BLANCOU 1949). BEST and EDMOND-BLANC (1969) following DOLLMAN (in LYDEKKER 1926) have suggested that *radcliffei* differs from *caffer* in having smooth horn-bases without transverse ridges, but taking wear into account, northern and southern savanna specimens examined in the British Museum all have more or less equally rough horn bases, and there seems to be no evidence that buffaloes from Uganda and Kenya can be distinguished from those of, say, Zambia or Mozambique. *Radcliffei* should be regarded as a synonym of *caffer*, and DOLLMAN (in LYDEKKER 1926) though continuing to recognise it as a distinct subspecies gives a succinct review of the validity of the many other names based on Eastern and Southern savanna buffaloes. CHRISTY (1924, 1929) refers to buffaloes of the *nanus* group from the Sesibwa (Seziwi) swamps between Lakes Kyoga and Victoria in Uganda. These animals may represent another enclave of forest buffaloes within a savanna zone.

From a little further south in Kiagwe (Chagwe) MATSCHIE (1906) named a race *neumanni* which was wrongly assigned to "*Bubalus nanus*" by CHRISTY (1929). With a horn span of 890 mm, the type is best relegated to *caffer*, as clearly implied by LYDEKKER (1913). DOLLMAN (in LYDEKKER 1926) considered it to be a synonym of *radcliffei*. The status of buffaloes in southeast Uganda must remain uncertain until CHRISTY's observation is confirmed or refuted.

g. Congo forest buffaloes

Small buffaloes from the Ituri forest described as *Bubalus adolfifriederici* by MATSCHIE (1918) are identified by their short and relatively stout horns, though in skull length they are not atypical for the *nanus* group (Table 2). *Adolfifriederici* is easy to distinguish from other populations of the *nanus* group mainly because of the absence of records from intervening areas in Kivu or Kasai. The populations are as much entitled to subspecific recognition as is *aequinoctialis*, but if they are formally given such status, following SCHOUTEDEN (1946), then it would probably be necessary to recognise further subspecies within the *nanus* group.

h. Albertine Rift

Large savanna buffaloes (*aequinoctialis* or *caffer*) come in close contact with small Congo forest beasts along the Western Rift (figure 9), or where savanna spills across the line of the Rift into the Congo basin, notably between Lakes Kivu and Edward. Buffaloes of the two groups occur in the Albert National Park, Congo Kinshasa. DALIMIER (1955) gives skull measurements which show modes for maximum length at about 450 and 500 mm, confirming the existence of two distinct populations in the

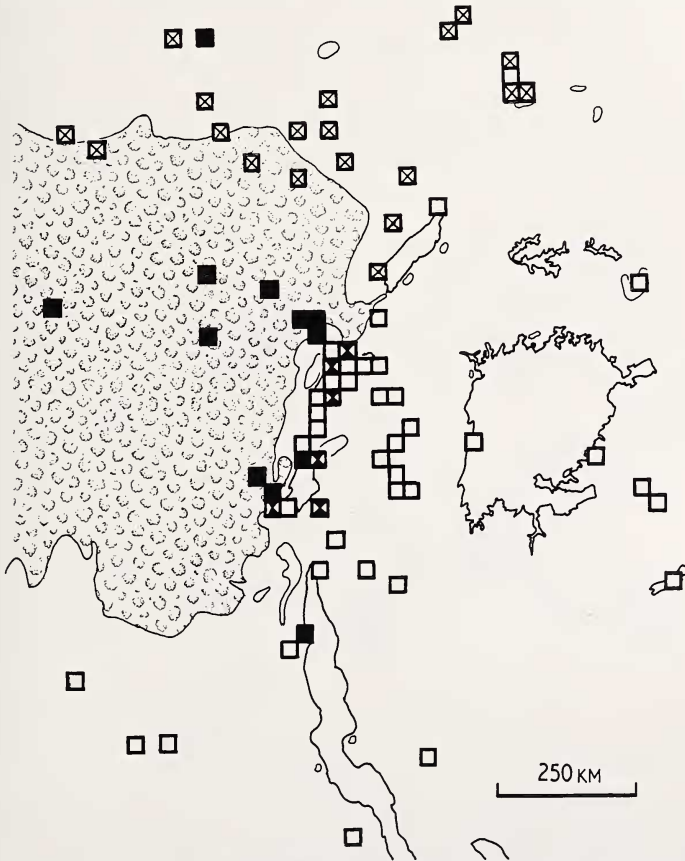


Fig. 9. Map of the Western Rift and Great Lakes region of East Africa to show distribution records of buffaloes assigned to various subspecies or regarded as intergrades. Symbols as in figure 8. Forest areas shaded

area. BOURLIERE and VERSCHUREN (1960) illustrate *nanus*-type animals from the forest and *caffer* buffaloes from the savanna, photographed within the neighbourhood of the park.

Intergradation between forest and savanna buffaloes is known from the Queen Elizabeth National Park, Uganda, as well as from the Albert Park, but it has been described only briefly, mostly by noting the existence of the red morph or the variability of horn shape in apparently hybrid stocks (FRECHKOP 1943, VERHEYEN 1954, BERE 1958, 1962; BOURLIERE and VERSCHUREN 1960, CURRY-LINDAHL 1961, SIDNEY 1965). In certain cases, these red buffaloes may have become red by soil staining (CURRY-LINDAHL 1961). Other red animals may be immature savanna buffaloes that will eventually lose the reddish tint as they mature. Nevertheless many observations probably do indicate that there is hybridisation and intergradation between forest and savanna buffaloes. From the examination of skulls from the Rift zone, some are found to be morphologically intermediate between *nanus* and *caffer* in character.

These intermediates include *Syncerus caffer mathewsi* and *S. c. cottoni* (see figure 10). The latter was wrongly assigned to "*Bubalus nanus*" by CHRISTY (1929) and subsequently by ALLEN (1939), and though LYDEKKER (1910) clearly indicated that it is a large buffalo, of the size of *caffer*, he mistakenly assigned a cow from the French Congo to *cottoni*. The type of *cottoni*, from Lake Edward (PCM Cong. 316), has the skull within the mounted skin, but it has been possible to examine a topotypic skull (PCM Cong. 326). These specimens are very much larger than the type of *mathewsi* and fall into the size range of the *caffer* group, indeed another specimen (PCM Cong. 412) from a nearby locality had the longest skull measured in this study. The horn span of these specimens is proportionally small, however, and the horns tend to lie in the facial plane, instead of being deflected below the skull (table 2,

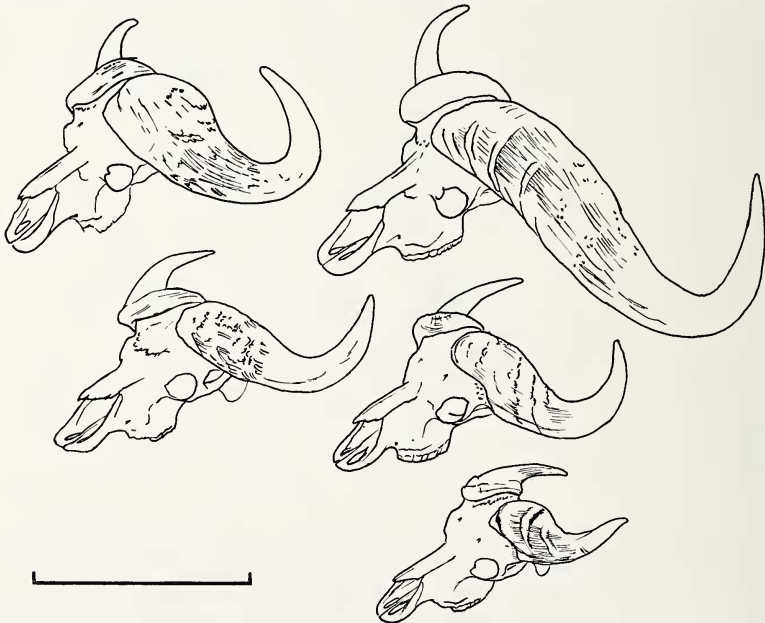


Fig. 10. Skulls of forest and savanna buffaloes from (top left to right): Mt Elgon, Uganda/Kenya border (*Syncerus caffer caffer* — BM 34.4.1.1.171); Amala river, Kenya (*S.c. caffer* — BM 29.8.2.1); Kasindi, Lake Edward, Congo Kinshasa (topotype of *cottoni* — PCM Cong. 326); Mfumbiro, northeast of Lake Kivu, Ruanda (type of *mathewsi* — BM 4.5.19.1); Beni Ituri forest, Congo Kinshasa (*S.c. nanus*, but referable to *adolffriedrici* — BM 30.11.11.427). Scale indicates 0.5 m

figure 10). They are thus similar to those of the much smaller *mathewsi* type (BM 4.5.19.1) from the Virunga volcanoes beyond Lake Kivu. In the shape of the horns and in dimensions this specimen is nearly a facsimile of *brachyceros*, but not, emphatically, of *aequinoctialis* as might be suggested by BLANCOU's 1954 classification (Table 1). A male from the Semliki valley (BM 25.5.24.1) is intermediate in skull size between *cottoni* and *mathewsi* but the horns are more of the *caffer* type. SCHOUTEDEN (1946) figures a *mathewsi*-sized male from Lake Edward, while CHRISTY (1924, figure 79) illustrates a large "*cottoni*" from Kasenyi, Lake Albert.

These Rift Valley buffaloes thus show a wide range of variation, and it does not seem reasonable to follow ROOSEVELT and HELLER (1922) in placing them all under *aequinoctialis*. Indeed on a typological basis they would be assigned to several subspecies. As they occur over such a narrow zone (figure 9) between the ranges of savanna and forest races they are best regarded as intergrades which occur in a variety of habitats. BLANCOU (1954) regarded *mathewsi* as a long-haired montane-forest race of buffalo. GYLDENSTOLPE (1928) and CURRY-LINDAHL (1951) recorded *mathewsi* from montane forests in Ruanda (Virunga, Rugege) and Congo Kinshasa (Kahuzi), but made no special reference to morphological features beyond noting the relatively short horns. Other intergrades, including "*S. c. cottoni*" have been obtained from savanna regions.

V. History of the species

CHRISTY (1929) noted the clinal transition between forest and savanna buffaloes of his species *Bubalus nanus*, but believed these animals were clearly differentiated from the *caffer* group. Although there are several errors of detail in his conclusions, CHRISTY's views are broadly substantiated here. CHRISTY explained the present day pattern of geographical variation by suggesting that southward recession of the West African forest belt at an unspecified date, leaving open areas of savanna, had led to differentiation of a western savanna variety of *nanus* (his "*aequinoctialis*") and he considered the sedentary nature of buffaloes had promoted such direct response to a changing environment. Before the differentiation of "*aequinoctialis*", the open-country *caffer* group had evolved (from forest buffaloes?) at a time when the East African savanna had experienced its apparently earlier phase of deforestation. The Rift system had encouraged this differentiation, during which *caffer* populations had expanded in range towards South Africa. CHRISTY's analysis can be traced back to earlier ideas about the origin of the East African savanna (see for example LÖNNBERG 1912), established on zoogeographical evidence with little support from geological data on the Pleistocene vicissitudes (MOREAU 1966).

MALBRANT (1935) took CHRISTY to task for the firmness of his separation of buffaloes into two species. He recognised that intermediate forms (not to be regarded as a third group of species) were distributed over a wide area (not specified by MALBRANT). He assumed there were once two quite distinct kinds, a small forest population and a large savanna one (*nanus* and *caffer* respectively). Recession of the forest encouraged the development of larger individuals on the periphery of *nanus*' range as well as expansion of the range of *caffer*. These events encouraged hybridisation between the two populations, and nowadays colour and horn polymorphism are to be explained by the segregation of characters in populations of mixed origin. The original *caffer* population has been little affected by interbreeding, but black buffaloes, with *caffer* "blood", are known from the depths of the forest, and thus the proto-*nanus* appears to have been adulterated by introgression to a greater extent. MALBRANT makes no attempt to explain the original divergence of *nanus* and *caffer*.

BLANCOU (1954) was not satisfied with these ideas. He conceded that recession of

the forest had an influence on buffalo populations, but pointed out that whenever this occurred, the vegetation belts must have already arrived at their present *relative* distributions and somewhere in Africa savanna habitats would long have been available for buffalo. In other words, forest recession was not sufficient cause for the evolution of savanna populations. He did not accept that semi-species of buffalo were completely separated at any time but suggested instead a gradual differentiation of savanna populations from the more primitive forest buffalo as the latter became more and more adapted to open country conditions and changes in diet. The colour forms represent a polymorphism and do not reflect "hybridisation".

There is a similarity between the geographic variation of the buffalo and that of the bushbuck (*Tragelaphus scriptus*), bushpig (*Potamochoerus porcus*) and elephant (*Loxodonta africana*). In these four species there are distinctive forest and savanna forms, predominantly reddish and blackish respectively in the artiodactyls. At least in some cases they show secondary intergradation along the western Rift (FRECHKOP 1943) and meet, apparently without gradual intergradation, along the forest border in Kasai (see maps in SCHOUTEDEN 1946). The savanna forms in West Africa have greater affinity with the forest representatives than with the savanna subspecies of eastern and southern Africa. There is some doubt as to whether all savanna elephants of West Africa are of the "forest" type, but only in the buffalo does there seem to be a case for the recognition of separate West African forest and savanna subspecies. The position of the three other animals in the Tchad area has not been clearly established.

It seems reasonable to surmise that in these four species gene flow between the southern savanna stocks and the parent forest populations was interrupted at some time and subspecies were able to differentiate more fully. The sharp distinction between buffaloes of the *caffer*-group and adjacent populations provides support for this idea. The West African savanna herds never lost reproductive contact with forest animals and may indeed have colonised the savanna biome independently following a phase of impoverishment (through extinction?) of the West African savanna fauna (MOREAU 1966, p. 135).

The expansion of Lake Chad into the Chari basin during the late Pleistocene must have divided western populations of savanna animals from eastern congeners. Buffaloes of the *brachyceros* and *caffer* groups were prevented from interbreeding and intergrading. Similarly populations of hartebeest (see MALBRANT 1936) and a number of birds were able to differentiate into distinctive semispecies (MOREAU 1966; HALL and MOREAU 1970). Segregation, this time between savanna and forest buffaloes, also appears to have occurred further to the east, aided perhaps by the fusion of lakes, vulcanism and the expansion of lowland and montane forests during the last pluvial period. Along the Albertine Rift there is definite evidence of the secondary intergradation made possible by subsequent reunion between the forest and savanna stocks. It is also possible that south of the Congo forest contact between forest and savanna buffaloes was not as free as now, but here we have seen that information is scanty. If we accept CARCASSON'S map (1964, figure 4) of vegetation distribution during a "pluvial period", we may suggest that montane forest expanding west to Angola cut off contact between forest and savanna buffaloes. Alternatively, lowland forest perhaps extended further south and the Luangwa Rift may then have played a part in isolating races from each other, just as it acts as a barrier between savanna populations of waterbuck today (ANSELL 1960).

These ideas take account of how forest and savanna populations may have become segregated but they do not explain how they differentiated in the first place. In discussing the evolution of *Brachystegia* and *Acacia* woodland avifaunas, BENSON and WHITE (1966) suggest that fragmentation of one habitat may be the major

factor encouraging the expansion of range into the surrounding vegetation type, presumably because contacts with the latter can become more frequent or even because it becomes impossible to maintain a home range entirely within one habitat. The effects of natural selection at the forest/savanna interface must be different from those within the forest itself and here we may have the preliminary basis for the evolution of a distinctive savanna form during the time that the sylvan populations infiltrate a more open environment.

In Africa, many cases of speciation have occurred within a single biome, and the first stages have involved the segregation of semispecies through division of the habitat (HALL and MOREAU 1970). The full differentiation of a new savanna species from its forest ancestor is more difficult to explain, for here the habitats of the diverging semispecies are always in contact and only under special circumstances is it possible to understand how gene flow could be arrested along the boundary between them. This might occur if the boundary is itself determined by some topographical feature which can act as a barrier.

Another possible explanation concerns the nature of the forest/savanna interface. If the forest is partly destroyed and fragmented at its junction with the savanna, then increased contacts between forest and savanna species may lead to hybridisation, as CHAPIN (1948) has suggested for the Paradise flycatchers. Conversely, if a sharply defined boundary to the forest is restored, then this might heighten the ecological contrasts between open and closed habitats and reduce contacts between the faunas. Through the reduction of gene flow, this might eventually lead to effective isolation of forest populations from their savanna relatives.

If buffaloes did make two more or less independent colonisations of the savanna biome, then the distinctiveness of the *caffer* group suggests that their differentiation occurred earlier. These animals may, however, be derivatives of the *brachyceros* stock, and indeed *S. c. aequinoctialis* is intermediate between *S. c. caffer* and *S. c. brachyceros*, both morphologically and geographically. This alternative theory implies that forest buffaloes were unable to make a widespread direct colonisation of the savanna south of the Congo forest, yet the southern Congo basin, with its complex interdigitation of forest and savanna, would appear at least nowadays to be an ideal area for sylvan populations to make contact with the savanna and to evolve into that habitat.

It must be admitted that dealing with the history of a complex pattern of geographic variation is very difficult, and details of the movements of vegetation zones and their effects on clines and disruption and reunion of populations can only be guessed at in the crudest way. The palaeontological evidence is quite insufficient, but bearing in mind the great morphological differences between forest and savanna buffaloes today, it seems reasonable to suggest that the extinct genera *Pelorovis* and *Homoioceros* may eventually be brought closer into the picture of speciation and diversification of these African bovids.

Acknowledgements

I am grateful to the following for allowing me to examine specimens in their care: C. POWELL COTTON and L. BARTON (Powell Cotton Museum, Kent); J. HILL and Dr. A. GENTRY (Natural History Museum, London); M. CISSÉ (I.F.A.N. Museum, Dakar), and to D. PAULY for translating the summary.

Summary

Previous classifications of African buffaloes, *Syncerus caffer*, are reviewed. Geographic variation in the species is summarised and it is shown that three groups of subspecies can be distinguished by horn configuration and size. There is little overlap of measurements between

the groups and each has a wide distribution corresponding to a distinct eco-geographic region of Africa:

1. *nanus*-group (small forest buffaloes; probably several subspecies);
 2. *brachyceros*-group (intermediate West African savanna buffaloes; one subspecies);
 3. *caffer*-group (large buffaloes of the southern and eastern savannas; two subspecies);
- A regional survey of buffalo populations is made. It appears that the *nanus* and *brachyceros* groups intergrade clinally but that there is secondary intergradation between *caffer* and *brachyceros* in the Chari Basin and between *caffer* and *nanus* along the Albertine Rift. The phenomena which may have initiated speciation in buffaloes are discussed and evaluated.

Zusammenfassung

Frühere Klassifizierungen des afrikanischen Büffels *Syncerus caffer* werden überarbeitet. Die geographische Verteilung dieser Art wird beschrieben, und es wird gezeigt, wie drei Gruppen von Unterarten an Hand der Form und Größe der Hörner unterschieden werden können. Diese Größen überlappen sich bei diesen Gruppen kaum, und jede Gruppe hat einen eigenen, großen Lebensraum, der einem bestimmten ökogeographischen Bereich entspricht:

1. die *nanus*-Gruppe (kleine Waldbüffel; wahrscheinlich mehrere Unterarten);
2. die *brachyceros*-Gruppe (vermittelnde Büffelart der westafrikanischen Savanne; eine Unterart);
3. die *caffer*-Gruppe (große Büffel der südlichen und östlichen Savannen; zwei Unterarten).

Es wurde eine regionale Erfassung der Büffelpopulationen durchgeführt. Es zeigt sich, daß die *nanus*- und *brachyceros*-Gruppen allmählich ineinander übergehen, aber daß es sekundäre Abstufungen gibt zwischen *caffer* und *brachyceros* im Chari-Becken sowie zwischen *caffer* und *nanus* entlang des Albertine-Erdspaltes. Die Ursachen der Ausbildung verschiedener Formen werden diskutiert und bewertet.

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Die Waldmäuse (*Apodemus*) Nepals¹

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Eingang des Ms. 15. 3. 1972

„In Nepal lebt anscheinend nur *Alsomys gurkha* (Thomas), eine auffallend dunkelgrau gefärbte Art“ schreibt ZIMMERMANN (1962) in seiner vortrefflichen Kurzrevision der Gattung *Apodemus*. Darin zeigt er, daß die Gliederung bei ELLERMAN und MORRISON-SCOTT namentlich für die östliche Paläarktis völlig falsch war und daß *Apodemus* in drei deutlich unterscheidbare Untergattungen mit unterschiedlichen Verbreitungsschwerpunkten zerfällt:

Apodemus mit *A. agrarius*, West- und Ostpaläarktis;

Sylvaemus mit *A. sylvaticus*, *A. flavicollis*, *A. mystacinus* und *A. microps*; nur Westpaläarktis;

Alsomys mit *A. speciosus*, *A. geisha*, *A. peninsulae*, *A. draco*, *A. latronum* und *A. gurkha*; nur Ostpaläarktis.

Ost- und Westgruppe berührten sich nach damaliger Kenntnis nur im Gebiet von Omsk, Novosibirsk und im Altai, wo *A. (Sylvaemus) sylvaticus* neben *A. (Alsomys) peninsulae* lebt. Ein weiteres Überschneidungsgebiet ist auf Grund des von J. M. 1969 und 1970 gesammelten Materials in Nepal zwischen den Arten *A. (Sylvaemus) sylvaticus* und *A. (Alsomys) gurkha* ausgebildet.

Unser Ziel ist es, die Populationen im Berührungsgebiet beider Arten morphologisch und ökologisch zu charakterisieren, zumal sich hier die ZIMMERMANNsche Gliederung von *Apodemus* voll bestätigt.

1. Ökologie und Verbreitung

Die vorliegenden Belege für *A. sylvaticus* bilden den Erstdachweis dieser Art für Nepal. Die Ostgrenze war bisher Phurkia in Kumaon (ELLERMAN 1961); die Neufunde ver-

¹ J. M. mit einem Jahresstipendium des DAAD und einer Sachbeihilfe der DFG. — Ergebnisse der Nepal-Reise 1969/70, Nr. 9. — Nr. 8: Senckenbergiana biol. 53 (1/2), 95—100, 1972.